

ON *CRASSIGYRINUS SCOTICUS* WATSON, A PRIMITIVE AMPHIBIAN FROM THE LOWER CARBONIFEROUS OF SCOTLAND

by A. L. PANCHEN

ABSTRACT. The unique holotype of *Crassigyrinus scoticus* Watson is almost certainly from the Viséan Gilmerton Ironstone of Scotland, as suggested by Watson. It consists only of the right side of a large primitive amphibian skull with a very long postorbital region. The pattern of dermal bones, which includes a well-developed preopercular, is intermediate in configuration between that of a rhipidistian fish and the earliest Amphibia, the ichthyostegids. *Crassigyrinus* may also have a rhipidistian-like course of the infraorbital lateral line system, but in the amphibian form of open sulci. The configuration of bones round the nostril is probably also similar to that of osteolepiform Rhipidistia. '*Macromerium*' *scoticum* Lydekker, a lower jaw from Gilmerton, formerly attributed to *Crassigyrinus*, is more probably *Loxomma allmanni*. *Crassigyrinus* is too large and far too late to be anything but a distant relict of the ancestral tetrapod stock. A new order of labyrinthodont Amphibia, the Palaeostegalia, is proposed for *Crassigyrinus*.

Crassigyrinus scoticus Watson is known only from the holotype, which consists of the right side of a large amphibian skull exposed in dorsal, external view on a massive block of ironstone. Only the cheek region and the side of the snout are present: the skull table, the middle preorbital region, and the left side are completely missing and nothing is known of the braincase or palate. In his original description Watson (1929) considered that only the maxilla, lacrimal, jugal, postorbital, squamosal, quadratojugal, and quadrate were preserved.

The specimen is registered as No. 1859.33.104 in the Department of Geology, Royal Scottish Museum (originally No. 272) and is from the Hugh Miller Collection. It is labelled 'Carboniferous Limestone' and is stated by Watson to come from the Midlothian region, but there are no further data. Watson attributed it to the Gilmerton Ironstone, Lower Limestone Group (Upper Viséan) on the character of the matrix, which is a nodular ironstone consisting of concretions of siderite in a hard dark grey shaly matrix. This is one type of matrix that occurs at the Gilmerton horizon.

Thanks to the very great kindness of Dr. A. H. V. Smith of the National Coal Board I have now some corroboration of Watson's opinion. A specimen of matrix from the holotype of *Crassigyrinus* was compared with a series of matrix specimens of known horizon kindly supplied by Dr. Mahala Andrews from the Royal Scottish Museum. The control specimens were from the Loanhead No. 2 Ironstone (Limestone Coal Group: Namurian A), the Gilmerton Ironstone, and the Dunnet Shale, Straiton (Upper Oil Shale Group: Viséan). The spore assemblages from the *Crassigyrinus* matrix were of Upper Viséan or Lower Namurian age and resembled those from the Gilmerton control specimens rather than those from the other horizons.

Crassigyrinus was placed by Watson in the labyrinthodont superfamily Anthracosauroidae of his grade Embolomeri, but *incertae sedis* as to family. It has already

been noted (Panchen and Walker 1961) that Watson's attribution to the anthracosaurs is probably to be regarded merely as an indication that he did not consider it to be a loxomatid, the other group of his 'grade Embolomeri' and the only other common group of Carboniferous labyrinthodonts from Great Britain.

Watson noted two characters of the skull which are atypical of anthracosaurs; the great expanse of the skull immediately below the orbit and the extension of the maxillary bone to underlie the quadratojugal, thus separating the jugal from the jaw margin. They are, however, paralleled in several temnospondyl labyrinthodonts (Panchen and Walker 1961).

Romer (1947) suggested that as the preserved cheek region had apparently separated cleanly from the missing skull table there might have been a kinetic separation of table and cheek of the anthracosaur type in the complete skull. In his classification of labyrinthodonts he placed *Crassigyrinus* with *Anthracosaurus russelli* to comprise the family Anthracosauridae. This grouping is retained but with expressed doubt in the current edition of *Vertebrate Paleontology* (Romer 1966). The association was based on the common possession of an unusually long suspensorium.

It is clear, however, that *Crassigyrinus* is not a member of the Anthracosauridae because of the small, relatively uniform teeth which contrast strikingly with the massive dentition of *Anthracosaurus* with its strong canine 'peaking' (Chase 1963, Panchen 1970). The present study was undertaken in an attempt to determine the affinities of *Crassigyrinus* for my monograph on the Anthracosauria (Panchen 1970). The exposed surface was further developed with an Industrial 'Airbrasive' unit to remove all residual matrix, and, as a result, I was able to report that *Crassigyrinus scoticus* was an extremely primitive amphibian which merits the fuller redescription given here.

An amphibian lower jaw, described by Lydekker (1890) as *Macromerium scoticum*, has also been tentatively ascribed to *Crassigyrinus* by several authors and is therefore also redescribed.

DESCRIPTION—SKULL ROOF

The holotype of *Crassigyrinus* (text-fig. 1, Pl. 16, fig. 1) represents a skull of similar size to that of *Anthracosaurus russelli* Huxley (Panchen 1970) and because of the relationship between them suggested by Watson and by Romer the latter specimen is a useful standard of comparison. *Anthracosaurus* also represents a primitive labyrinthodont and a comparison of proportions and detailed bone pattern highlights the unique features of *Crassigyrinus*.

Crassigyrinus is characterized by the very long postorbital cheek region, so that the posterior border of the orbit is more than half-way forward from the back of the quadrate to the anterior end of the specimen. Preservation probably extends to the tip of the snout. The orbit is very large and, as far as preserved, is a parallelogram

EXPLANATION OF PLATE 16

- Fig. 1. *Crassigyrinus scoticus*, holotype. R.S.M. 1859.33.104, $\times \frac{1}{2}$.
 Fig. 2. '*Macromerium*' *scoticum*, holotype. B.M. (N.H.) R310, $\times \frac{2}{3}$.



PANCHEN, primitive amphibian

in outline, with the parallel anterior and posterior borders inclined backwards towards the midline and the ventro-lateral border sloping upwards towards the back of the orbit. The dorso-mesial border is missing.

Behind the orbit the long cheek region tapers towards the massive quadrate region, while anteriorly the snout is, by labyrinthodont standards, exceptionally broad and short. Significant dimensions are compared with those of *Anthracosaurus* in Table 1: all measurements in both cases are as nearly as possible in the plane of the skull roof.

TABLE 1. *Crassigyrinus scoticus* and *Anthracosaurus russelli* holotypes

	<i>Crassigyrinus</i>	<i>Anthracosaurus</i>
Overall length (centre-snout to quadrate condyle)	340 mm	420 mm
Back of orbit—quadrate	190 mm	175 mm
Ventral border of orbit—maxillary margin (minimum transverse distance)	65 mm	c. 30 mm
Length of orbit (ant.—post.)	50 mm	c. 45 mm
Depth of orbit (mesial—lateral)	c. 45 mm	35 mm
Depth of cheek immediately behind orbit	105 mm	c. 70 mm

After cleaning with the Airbrasive unit the sutures between individual dermal bones became very clear and the pattern behind the front of the orbit is established beyond reasonable doubt. There is, however, some uncertainty about the configuration of the snout region due to compression, erosion, and distortion.

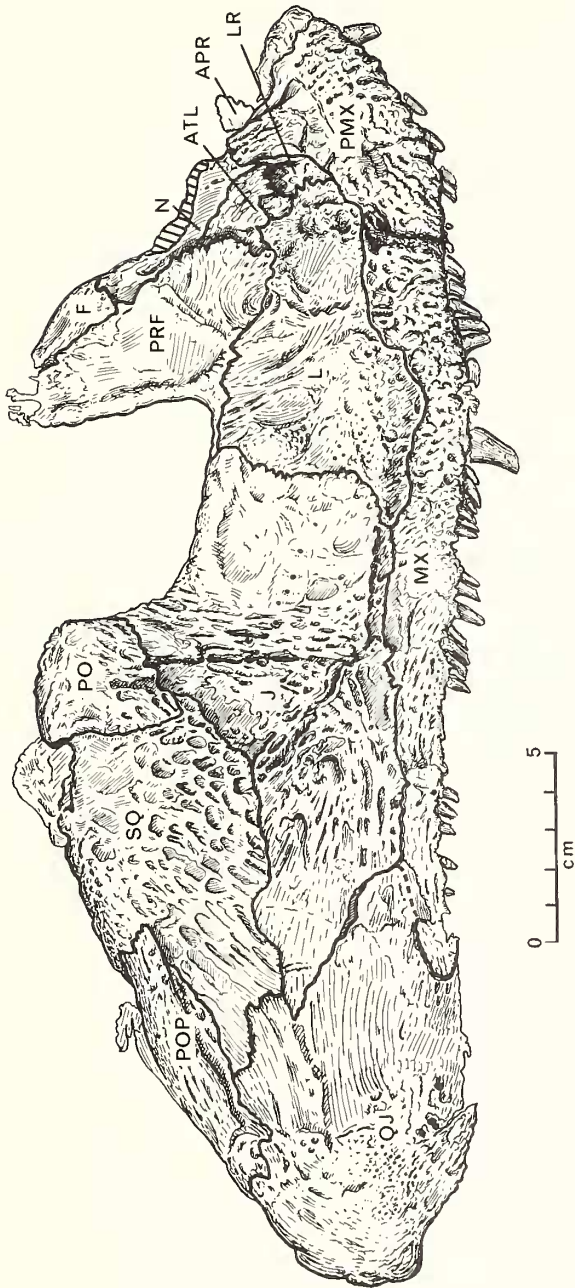
The preserved bones of the cheek region comprise the jugal and quadratojugal and above them the postorbital, squamosal, and a bone that can only be identified as preopercular. The boundary sutures of all the bones were traced throughout.

The anterior border of the jugal, formed by a long transverse suture with the lacrimal, is exceptionally far back for a labyrinthodont, being well behind the level of the front of the orbit and turning further posteriorly at its ventro-lateral end. The lacrimal thus extends behind the middle of the orbit. Ventrally the jugal is completely excluded from the jaw margin by the maxillary, as already noted, but its postero-dorsal corner, situated in the suture with the quadratojugal, extends just posteriorly to the maxillary.

The surface of the jugal is not strongly ornamented, but there is reason to think that there has been considerable erosion of the surface. The area below the orbit is certainly eroded but below the postorbital and squamosal a small irregular pit and ridge ornament is preserved. The ornament is elongated in a transverse direction below the latter bone, but is vertical below the former.

The only reasonably clear traces of the lateral line system are preserved on the jugal and then with less than absolute certainty. A series of deeper elongate pits forming a vertical line from the suture with the postorbital to that with the maxillary may mark the descending course of the infraorbital sulcus which is then reflected forward as a groove just above the maxillary suture and runs forward to continue its course more doubtfully on the lacrimal.

The course of the jugal sulcus may be marked by a line of elongate pits running



TEXT-FIG. 1. *Crassigyrinus scoticus* Watson, holotype as preserved ($\times \frac{1}{2}$). APR, anterior postrostral; ATL, anterior tectal; F, frontal; J, jugal; L, lateral rostral (septomaxillary); MX, maxillary; N, nasal; PMX, premaxillary; PO, postorbital; POP, postopercular; PRF, prefrontal; QJ, quadratejugal; SQ, squamosal.

obliquely upwards and backwards from a point just above the flexion of the infra-orbital sulcus, but there is no sign of its continuation on to the squamosal.

If these sulci are correctly interpreted this course follows that of the lateral line canals of *Eusthenopteron* in that the infraorbital sulcus is inflected forwards near the ventral margin of the jugal and the jugal sulcus originates well above the flexion. In this respect the pattern is more primitive than that of *Ichthyostega* in which the flexion is more dorsal and the jugal canal originates at its angle (text-fig. 3). On the other hand *Ichthyostega* still has the fish structure of its lateral line system with canals through the bone opening only by pores to the surface and in this respect is probably more primitive than *Crassigyrinus* (Jarvik 1952).

At first I was tempted to interpret a horizontal row of pores at about half-way down the jugal as signs of a hidden fish-like canal. Three pores on the lacrimal would then continue this series, but it now seems more probable that they all represent the remnants of an eroded ornament. Ironically if the grooves represent the lateral line system they follow the fish course but are in the amphibian condition, whereas the pores would follow the amphibian course but represent the fish condition.

The quadratojugal of *Crassigyrinus* is unusually large whether compared with that of rhipidistians or labyrinthodonts. Little of the quadrate is visible and some development in its expected position indicates that most of it is probably missing. However, the massive curvature of the back of the quadratojugal suggests that the quadrate condyle was of unusually large diameter. The surface of the quadratojugal is eroded, but antero-ventrally it shows a series of fine horizontal ridges which converge slightly posteriorly suggesting a centre of ossification near the back of the bone. Posteriorly there is an area of very fine pitting.

The postorbital is a quadrilateral bone with a transverse posterior suture with the squamosal. The configuration of these bones thus have an amphibian rather than a fish-like aspect, as does the extension backward of the jugal beyond the lower border of the squamosal. The postorbital, again somewhat eroded, shows evidence of a coarse labyrinthodont pit and ridge ornament of the type better preserved on the squamosal.

The latter bone, together with the preopercular and possibly the quadratojugal, had a massive postero-dorsal exposure. This is formed by the dorsal border of the posterior half of the bone being inflected inwards through a right angle. In front of this inflected region an inset rounded piece of bone projects above the main squamosal and is apparently an overlap area for the skull table.

The ornament of the main, lateral part of the squamosal is well preserved ventrally and consists of a massive and irregular pit-and-ridge system of labyrinthodont type. The ornament converges towards a point just below the overlap area and the pits have steep proximal walls but slope up gradually distally.

The preopercular occupies exactly the same morphological position as that in the rhipidistian *Eusthenopteron* (Jarvik 1944) and that in *Ichthyostega*. It forms the posterior part of the postero-dorsal border of the cheek region and sutures with the squamosal and quadratojugal. The suture between the latter two bones thus runs perpendicularly to its ventral border. It is relatively a considerably larger bone than that of *Ichthyostega* but does not quite reach the proportions of that in *Eusthenopteron*. Because of the massive nature of its dorsal shelf compression of the specimen

has forced the dorsal part of the bone outward relative to the ventral part, but the lateral surface was probably flat in the intact skull. The preopercular runs dorsal to the squamosal for about half the length of the latter and its anterior squamosal suture is clearly marked on both lateral and dorsal surface.

The sutures bounding the lacrimal are also clear: the position of its posterior, jugal suture has already been commented on. Ventrally it has an irregular suture with the maxillary. Dorsally, as in the position of the jugal suture, its position and relationships are an accurate intermediate between those in *Eusthenopteron* and *Ichthyostega*.

The lacrimal of *Eusthenopteron* forms the major part of the ventral rim of the orbit, while that of *Ichthyostega* is excluded by the junction of jugal and prefrontal above it, as in anthracosaurs. In *Crassigyrinus* the lacrimal just fails to reach the orbit dorsally as there is a jugal-prefrontal contact along the orbital rim.

The surface of the lacrimal is deeply contoured in such a manner, which may be in part due to compression, that the form of its hidden mesial surface is impressed on the outside. Posteriorly, below the front of the orbit, there are two convex areas. The lower one is horizontally oval with an eroded ornament, the upper a vertical oval with a shallow trough in front. A concave area between them carries the pores which were thought to mark the course of the infraorbital canal while the possible sulcus runs below them.

The remaining anterior area of the bone forms two further troughs of badly eroded bone separated from one another and from the first trough by low ridges, and in front of them a raised eroded area with two deep pits.

The prefrontal forms the whole anterior border of the orbit, along which it is raised as a thickened rim, and extends along the ventral border to meet the jugal. Ventrally its suture with the lacrimal was traced throughout, as was its anterior boundary. The surface of the bone shows little ornament and is probably eroded.

The form of the maxillary is very similar to that of large anthracosaurs such as *Eogyrinus* (Panchen 1972b) and *Anthracosaurus*. It is convex in a transverse plane and is irregularly ornamented anteriorly. In the posterior half of the bone the ornament is more regular and is elongated into a series of longitudinal grooves. The bone surface is, however, considerably eroded for the final quarter of its length.

As has already been noted the maxillary completely excludes the jugal from the jaw margin and has a considerable backward extension below the quadratojugal. Anteriorly the maxillary underlies all but the extreme anterior end of the lacrimal. The suture between the maxillary and premaxillary is a transverse line. All but the dorsal half-centimetre is easily traced. Both bones curve in towards the suture so that the latter is situated along the floor of a deep but irregular groove. Dorsally this groove runs into a pit with disrupted bone in its floor and it is here that the suture cannot certainly be traced.

I was originally inclined to interpret this pit as the nostril: this would then terminate a naso-labial groove of the type common in early tetrapods (Panchen 1967, 1970). While this interpretation is still possible it is not the one I now favour.

The premaxillary is a massive bone ornamented like the front of the maxillary. Preservation apparently extends to its median edge and a possible fragment of the left premaxillary with their joint midline suture is present anteriorly.

The premaxillary is much wider from top to bottom throughout its length than the maxillary. In addition it bears a massive dorsally directed process near the front. In *Eusthenopteron* a similar but relatively smaller process of the premaxillary rises to meet the nasal series on each side and to separate the anterior tectal from the median anterior postrostral.

In *Crassigyrinus* if the process is viewed from the front it is seen to be paralleled by another more mesial to it and also apparently formed from the premaxillary. The matrix-filled groove between them was interpreted by Watson as the nostril, on the assumption that the whole bone I have called premaxillary was the anterior end of the maxillary and that the premaxillary was missing.

I have now cleaned the groove between the two processes: the bottom of the groove is marked by a line of junction which indicates that the two processes are separate and may originally have had an aperture between them. However, if the premaxillary is correctly identified and the outer process is part of it (there is a crack across the base of the process) then interpretation of the space between the processes as the nostril is very difficult.

It seems more probable that the two premaxillary processes buttressed a massively developed snout region and it is not impossible that the inner one pertains to an ossified nasal capsule. Presumably an anterior postrostral, present in both *Eusthenopteron* and *Ichthyostega*, was situated in front of the outer process. A fragment of what may be this bone is present in the specimen.

The bony area between the prefrontal and the premaxillary process is disrupted and difficult to interpret which is particularly unfortunate as, by analogy with *Eusthenopteron*, the nostril (fenestra exonarina anterior—Jarvik 1942) should be situated in that region.

The dorsal part of the suture forming the anterior boundary of the prefrontal is with a strip of bone which presumably represents the frontal. A short suture forming the antero-ventral boundary of the latter bone can be traced with reasonable certainty. Below this the nasal appears to have been twisted so that its inner, ventro-mesial surface is exposed to view with the broken posterior edge showing at the front.

However, there is a further area of bone between the nasal and the front of the lacrimal. Most of this appears to be occupied by a poorly preserved bone whose relationships are exactly those of the anterior tectal of *Eusthenopteron* and *Ichthyostega*. A small piece of raised bone bordering the front of the lacrimal may be the only part of the anterior tectal whose periosteal surface is preserved or may be an extra ossification.

The ventral edge of the anterior tectal borders what may be the nostril, although I am not entirely convinced of this. The nostril is an oval area entirely occluded by bone. This bone is presumably septomaxillary, or in fish terms the processus dermintermedius of the lateral rostral (Jarvik 1942, Panchen 1967) and, as in *Eusthenopteron*, the lateral rostral is exposed outside the cavity of the nostril as a triangle of bone between the lacrimal and the premaxillary, and bordering the nostril ventrally.

The dentition of *Crassigyrinus* is distinctive. Twenty-five small teeth are preserved on the maxillary. Those which are intact are, as Watson notes, shell or bullet-shaped but some show a slight turning back of the tip. They are fairly uniform in size with a slight but not consistent diminution towards the back. The longest is 10 mm to

the tip of the crown and has a basal diameter of 4 mm. The shortest is about half that length and has a diameter of 2.5 mm.

It is probable that a much larger number of maxillary teeth was originally present. Those preserved are in groups and are very close set, accounting for not much more than half of the maxillary length, so that an original count of about 40 including replacement pits is not improbable.

In addition to the maxillary teeth a large palatine tusk is visible below the maxillary at the level of the back of the lacrimal. The tip of the crown is broken off and presumably the whole is not visible but the maximum diameter is 9 mm and the visible length 15 mm.

Only 6 widely separated and poorly preserved premaxillary teeth are visible. The anterior one is the largest and most complete. The tip is broken off but the remainder is 9 mm long and has a diameter of 5 mm so that it is somewhat larger than the maxillary teeth. The others are comparable in size to the latter.

'*MACROMERIUM*' *SCOTICUM* LYDEKKER

'*Macromerium*' *scoticum*, known only from the holotype, consists of an incomplete right jaw ramus preserved with the lateral surface exposed on a block of ironstone. The specimen is from the Gilmerton Ironstone and is registered as R310 in the British Museum (Natural History).

It was briefly described by Lydekker (1890) who noted that while its shape favoured attribution to *Loxomma* the apparent poor development of the ornament was more like that of *Anthracosaurus*. He finally attributed it to Fritsch's (1889) genus *Macromerion*. The (invalid) change in the termination of the generic name represents Lydekker's policy of latinizing all genera.

He attributed the specimen to *Macromerion* on the character of the teeth but whatever the nature of the dentition the attribution is invalid. Fritsch's original genus contained a variety of unrelated species, including 2 anthracosaurs, probably 2 temnospondyls, and a pelycosaur. It may properly be used to refer to the latter (Romer 1945, Panchen 1970).

M. scoticum was discussed by Watson (1929), who noted the impossibility of its reference to *Macromerion* and concluded that it was 'not quite inconceivable' that it should be referred to *Crassigyrinus*. On balance, however, he considered that there was insufficient evidence even to determine its sub-ordinal position with safety and unless subsequently associated with a skull 'it had better be ignored'.

Romer (1947) noted the possibility of association with *Crassigyrinus* and more recently I noted a similarity in the teeth (Panchen 1970). I have now had the opportunity to further develop and study the holotype of *M. scoticus*.

The exposed surface of the specimen was covered with a thin film of matrix and this has been completely removed by 'Airbrasive' treatment. The surface is much eroded but the sutures can now be determined with ease. The specimen includes the whole of the jaw ramus with the exception of the articular region. Thus the articular bone and part of the surangular and angular are missing, as is the extreme posterior end of the dentary: however, preservation probably extends beyond the back of the dentary tooth row. In addition there is newly exposed a mass of badly eroded

bone behind the jaw which may include the articular region but more probably pertains to the rest of the skull (text-fig. 2, Pl. 16, fig. 2).

The shape of the jaw, as noted by Lydekker, is very reminiscent of that of a loxomatid and development shows that the pattern of dermal bones is fairly close to that of the Coal Measure loxomatid *Megalocephalus* (Watson 1926, Tilley 1971).

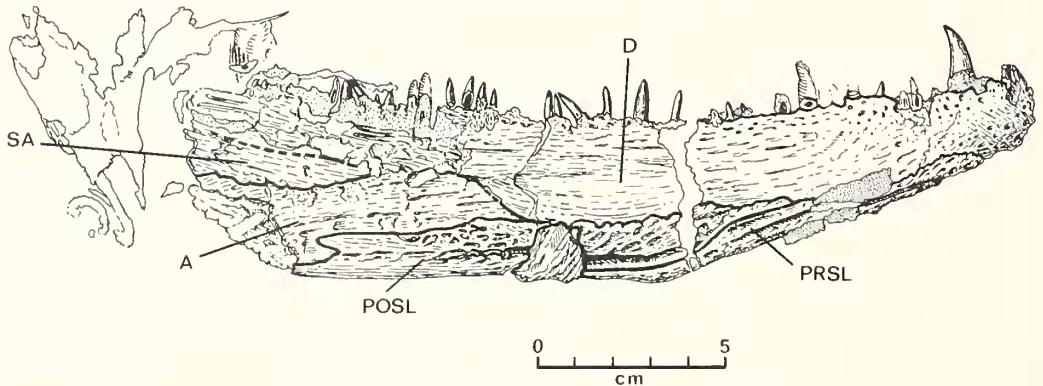
The dentary extends further ventrally, particularly in front of the anterior apex of the angular, than Watson's restoration of the jaw of *Megalocephalus* ('*Orthosaurus*') suggests, but corresponds more closely to Tilley's restoration of the Coal Measure form. The surface of the dentary appears moderately well preserved except posteriorly where it is dorsal to the angular and surangular.

Anteriorly, in the region of the symphysis, a shallow and irregular ornament is punctuated by small but deep pits. The rest of the bone is ornamented by shallow and irregular longitudinal grooves. If this appearance is not due to erosion it would appear to constitute a striking difference from the regular honeycomb ornament characteristic of the skull of *Megalocephalus* and many other temnospondyls. However, on inspection of the jaw rami of *Megalocephalus* in the Hancock Museum it is seen that the posterior part of the dentary also bears a lateral ornament of longitudinal grooves immediately below the tooth row. This may be seen in G15.46, a complete jaw ramus, and in G15.39. More anteriorly the 'Macromerium' ornament could well have been produced by erosion of the *Megalocephalus* type of dentary.

Only an anterior wedge of the surangular is preserved in 'Macromerium' between the dentary above and the angular below. Its line of junction with the dentary, which overlaps it considerably, is not preserved throughout because of the disruption of that bone. The surface of the surangular is ornamented only with fine longitudinal striae in contrast to *Megalocephalus* where the typical ornament is more or less developed in this region.

This is also the case with the angular which extends considerably further forward, as in *Megalocephalus*, but in the present specimen is underlain throughout its preserved length by the posterior splenial.

The 2 splenials form most of the ventral border of the specimen and, as in *Megalocephalus*, carry the conspicuous groove of the mandibular lateral line sulcus. The



TEXT-FIG. 2. *Macromerium scoticum* Lydekker, holotype as preserved ($\times \frac{1}{2}$). A, angular; D, dentary; POSL, postsplenial; PRSL, presplenial; SA, surangular.

ornament on the splenials is most strongly developed above the groove and is not apparently of the *Megalocephalus* type but bears some resemblance to that on the jugal and squamosal of *Crassigyrinus*.

The suture between the splenials is so oblique as to be almost horizontal, beginning far forward dorsally and running back for about 6 cm until it is lost below an extraneous piece of dermal bone on the surface of the specimen. Its exact course is duplicated in the *Megalocephalus* jaw G15.39.

The greatest contrast between '*Macromerium*' and the jaw of *Megalocephalus* lies in the size of the teeth. The dentary dentition of *Megalocephalus* consists of relatively large teeth, which in the case of the parasymphysial tusk and the teeth which alternate with the tusks on the palate, reach a height of some 30 mm. The smaller teeth are between 10 and 20 mm.

In '*Macromerium*', which represents a jaw of over two-thirds of the size of that of a typical *Megalocephalus*, the majority of the teeth vary between 5 and 10 mm. This disparity is reflected in the number of teeth or tooth sites which may be estimated at nearly 50 in '*Macromerium*' but less than 35 in *Megalocephalus*.

However, '*Macromerium*' has a well-developed parasymphysial tusk with a crown height of nearly 15 mm in exactly the corresponding position to that of *Megalocephalus*. It also has an adjacent pair of large teeth both broken off at the base of the crown. The anterior one, however, is represented by a good natural cast and had a similar crown height to the parasymphysial tusk. The pair of teeth are situated at about 4 cm from the tusk in a position corresponding to that of a very large tusk in *Megalocephalus*.

The size of the small teeth is approximately the same as that of the maxillary teeth of *Crassigyrinus* and their general shape is similar, being bullet-shaped and not markedly recurved. However, they are more slender and I am not now so impressed with the resemblance. In structure they appear to be of loxommatid type with anterior and posterior keels distally. The parasymphysial tusk is less strongly lanceolate than that of *Megalocephalus* and is recurved but bears the keels.

The known amphibian fauna of Gilmerton consists of *Pholidogaster pisciformis* Huxley, an anthracosaur skull attributed to it by Watson (1929) and Romer (1964), but certainly in error (Panchen 1970), *Crassigyrinus* and *Loxomma allmanni* Huxley. There is no possibility of attributing '*Macromerium*' *scoticum* to the first two. Its minor resemblances to the skull of *Crassigyrinus* do not now, after close study, seem to warrant association with that form and it seems unlikely that such a relatively shallow jaw should be associated with such a deep skull roof.

On the other hand attribution to *Loxomma* seems quite likely. The pattern of dermal bones is loxommatid, as is the general form. The presence and position of the parasymphysial tusk also corresponds and the form, if not the size, of the teeth is suitable. Nothing is certainly known of the dentition of *Loxomma allmanni* and only the premaxillary and anterior maxillary teeth are known in the Coal Measure species *L. acutirhinus* Watson (1929, Tilley 1971). The estimated total count for the upper tooth row in this case is only about 35–38 but a larger number of smaller teeth might well be regarded as a more primitive condition likely to be found in the Lower Carboniferous *L. allmanni*.

Thus apart from the character of the ornament '*Macromerium*' *scoticum* has the

characteristics of a loxommatid jaw. It should also be noted that in *L. allmanni* the character of the ornament is known only from the posterior skull table and finally that the 'Macromerium' jaw is of exactly the right size for the reconstructed skull length (Tilley 1971) of the contemporary loxommatid. Dr. Beaumont (*née* Tilley) has kindly inspected the 'Macromerium' jaw and endorsed its attribution to *Loxomma*. It, therefore, need no longer be considered in a discussion of the anatomy of *Crassigyrinus*.

DISCUSSION

The size and configuration of the dermal bones present in *Crassigyrinus* together with the proportions of the skull are the most primitive recorded in any amphibian and, as far as preserved, are almost exactly intermediate between those in a typical rhipidistian, e.g. *Eusthenopteron*, and the Devonian amphibian *Ichthyostega* (text-fig. 3).

Thus the preopercular bone is intermediate in relative size as is the squamosal. The jugal increases in both anterior and posterior extent in the fish-amphibian transition and also establishes a contact with the prefrontal: again *Crassigyrinus* shows an intermediate condition in this and in the position of the jugal-lacrimal suture.

The interpretation of the bones of the snout is not absolutely certain but again it appears to be intermediate and the lateral line system, if correctly interpreted, shows a primitive course otherwise known only in fish.

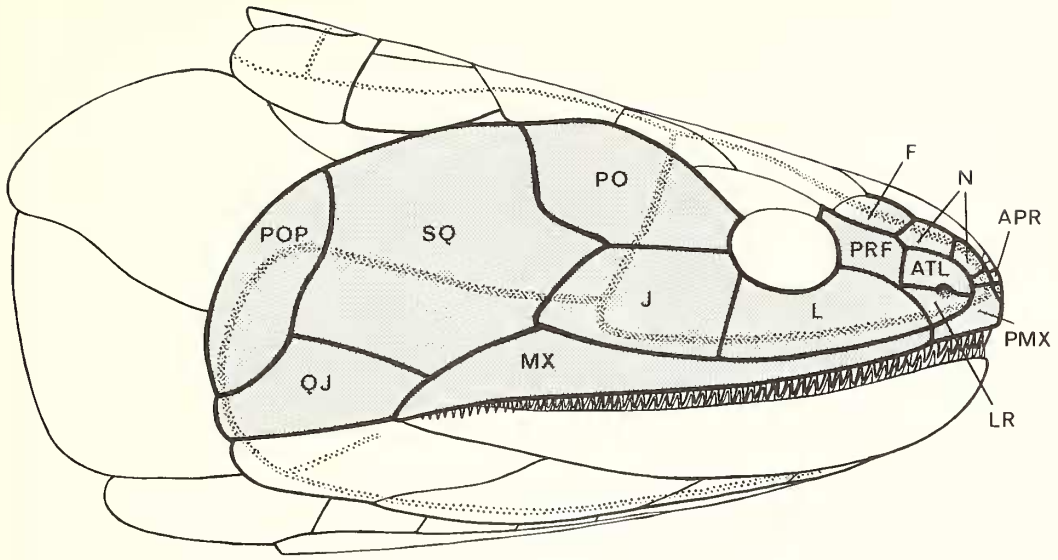
The proportions of the skull of *Crassigyrinus* as measured by the relative position of the orbit are also quite remarkable in being intermediate between those of *Eusthenopteron* and *Ichthyostega*.

There is, of course, no absolute certainty that *Crassigyrinus* is a tetrapod, but the characteristic features of massive quadratojugal and quadrate, large quadrilateral orbit, large prefrontal, and massive maxillary and premaxillary all suggest labyrinthodont affinity as does the nature of the dermal ornament and probably the lateral line sulci.

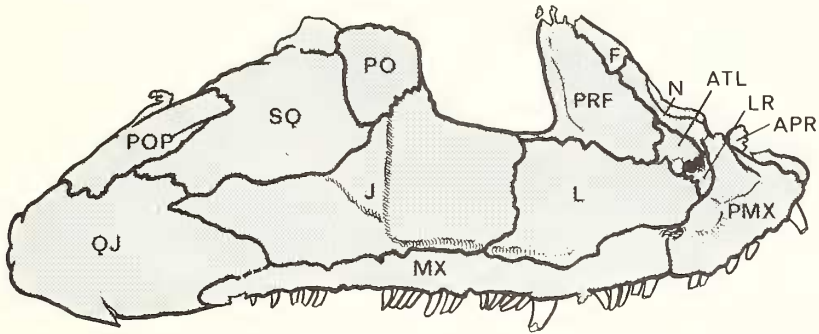
It is conceivable that the proportions of the skull of *Crassigyrinus* could have been due to a secondary migration forward of the orbits and that the interpretation given here of the fish-like snout is wrong. The presence of a preopercular bone is, however, incontestably primitive. Apart from *Ichthyostega* the only amphibian in which it is known, and then not with certainty, is the contemporary Devonian *Acanthostega* (Jarvik 1952).

In spite of these primitive characters *Crassigyrinus* is nevertheless a relatively late form and could not be more than a relict of any ancestral amphibian stock. Its large size and massive build is also in contrast to the small size to be expected in the common ancestor of reptiles and amphibians (Panchen 1972a).

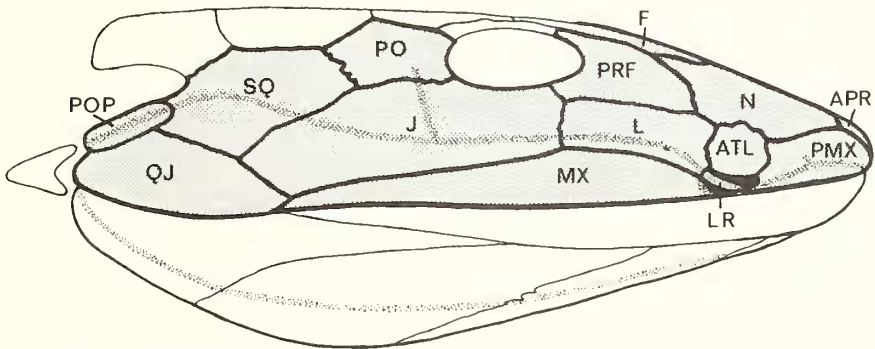
Thus the uppermost Viséan from which *Crassigyrinus* comes is dated at some 20 million years after the Devonian-Carboniferous boundary (Francis and Woodland 1964) whereas the origin of the amphibia was certainly well down in the Devonian. The age of *Ichthyostega* and *Acanthostega* is uncertain as direct correlation between the continental *Remigolepis* series from which they come and the standard marine



(a)



(b)



(c)

TEXT-FIG. 3. Skulls in right lateral view, reduced to same quadrate length. (a), *Eusthenopteron* (after Jarvik); (b), *Crassigyrinus*; (c), *Ichthyostega* (after Jarvik). (Region preserved in *Crassigyrinus* stippled.) APR, anterior postrostral; ATL, anterior tectal; F, frontal; J, jugal; L, lacrimal; LR, lateral rostral (septo-maxillary), MX, maxillary; N, nasal; PMX, premaxillary; PO, postorbital; POP, preopercular; PRF, prefrontal; QJ, quadratojugal; SQ, squamosal.

section has not been achieved. Säve-Söderbergh (1932) and Jarvik (1948, 1950) favour an Upper Devonian date. The nature of the vertebrate fauna of the *Remigolepis* series, notably the placoderms including the antiarch *Remigolepis*, as well as that of the overlying *Grönlandaspis* series support this conclusion. However, Westoll (1940, 1943) bases a Lower Carboniferous date on the agreed correlation of the underlying *Phyllolepis* series with the Dura Den horizon in Scotland. This is near the summit of the British continental Devonian and passes into the base of the Carboniferous without an apparent marked unconformity.

However, limb bones from Nova Scotia awaiting description by Dr. Baird demonstrate that well-developed tetrapods were already in existence in the Tournaisian or basal Carboniferous and support a long Devonian history for amphibia.

Assigning a taxonomic position to *Crassigyrinus* is difficult. As with the ichthyostegids it is probably to be assigned to the Labyrinthodontia, but should not be included in either of the major orders of that class, the Temnospondyli and the Batrachosauria (Antracosauria of Romer). Nor can it reasonably be included in the order Ichthyostegalia. It might be regarded as premature to erect an order for *Crassigyrinus* alone: nevertheless it must be placed taxonomically and I propose a new order of labyrinthodonts, the Palaeostegalia, characterized by the fish-like proportions of the skull in lateral view and the presence of a preopercular bone: also probably diagnostic are a lateral line system with amphibian sulci but with a rhipidistian configuration on the jugal, and a snout region whose bone pattern retains features of that of the osteolepiform Rhipidistia.

The order contains only *Crassigyrinus* in the monotypic family Crassigyrinidae.

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